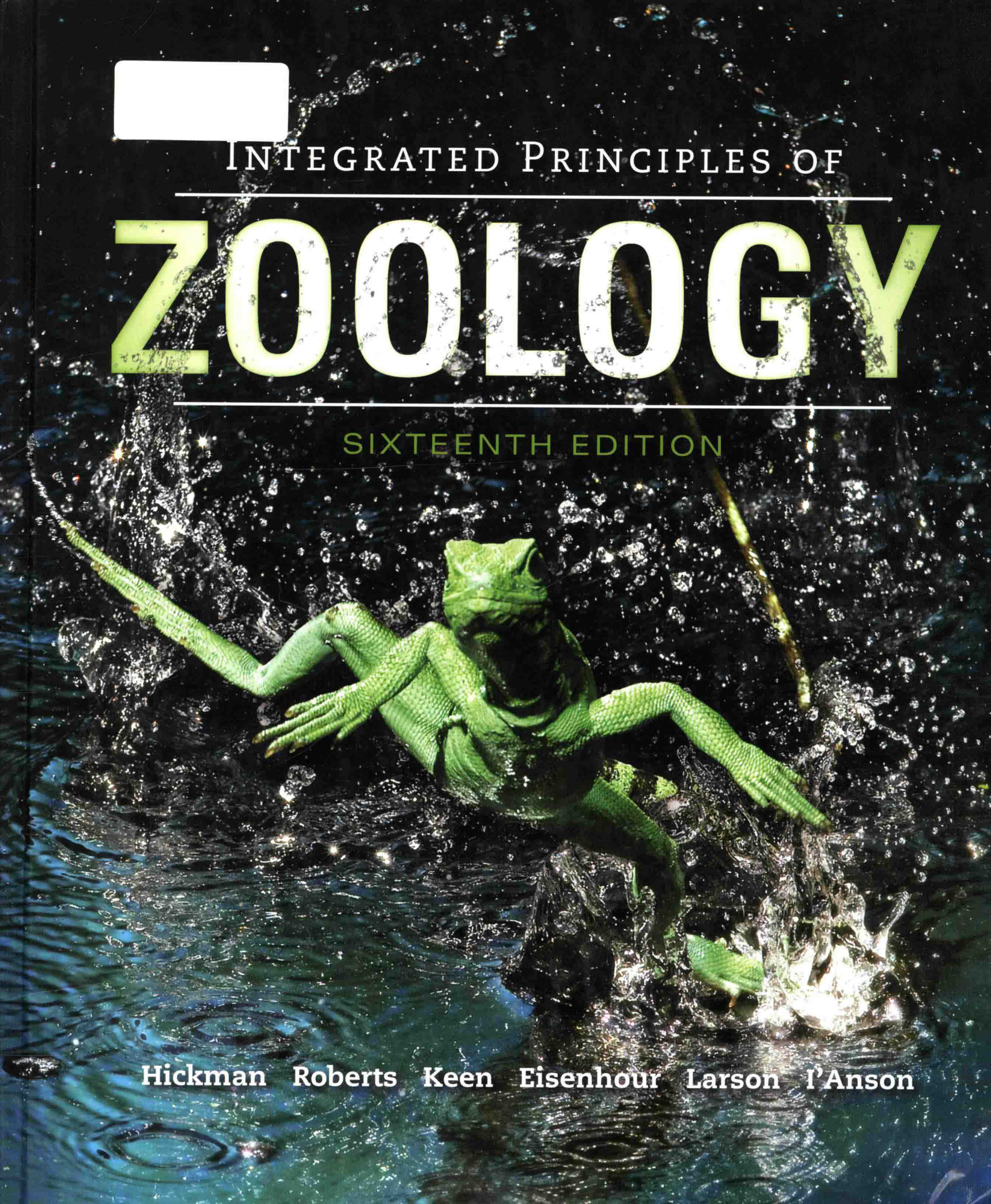
INTEGRATED PRINCIPLES OF
ZOOLOGY
SIXTEENTH EDITION
Hickman Roberts Keen Eisenhour Larson I'Anson

INTEGRATED PRINCIPLES OF

ZOOLOGY

SIXTEENTH EDITION

Cleveland P. Hickman, Jr.
WASHINGTON AND LEE UNIVERSITY

Larry S. Roberts
FLORIDA INTERNATIONAL UNIVERSITY

Susan L. Keen
UNIVERSITY OF CALIFORNIA – DAVIS

David J. Eisenhour
MOREHEAD STATE UNIVERSITY

Allan Larson
WASHINGTON UNIVERSITY

Helen I'Anson
WASHINGTON AND LEE UNIVERSITY

Original Artwork by
WILLIAM C. OBER, M.D.
WASHINGTON AND LEE UNIVERSITY
AND
CLAIRE W. OBER, B.A.
WASHINGTON AND LEE UNIVERSITY

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ABOUT THE AUTHORS

CLEVELAND P. HICKMAN, JR.

Cleveland P. Hickman, Jr., Professor Emeritus of Biology at Washington and Lee University in Lexington, Virginia, has taught zoology and animal physiology for more than 30 years. He received his Ph.D. in comparative physiology from the University of British Columbia, Vancouver, B.C., in 1958 and taught animal physiology at the University of Alberta before moving to Washington and Lee University in 1967. He has published numerous articles and research papers in fish physiology, in addition to co-authoring these highly successful texts: *Integrated Principles of Zoology, Biology of Animals, Animal Diversity, Laboratory Studies in Animal Diversity,* and *Laboratory Studies in Integrated Principles of Zoology.*

Over the years Dr. Hickman has led many field trips to the Galápagos Islands. His research is on intertidal zonation and marine invertebrate systematics in the Galápagos. He has published three field guides in the Galápagos Marine Life Series for the identification of echinoderms, marine molluscs, and marine crustaceans.

His interests include scuba diving, woodworking, and participating in chamber music ensembles.

Dr. Hickman can be contacted at:
hickmanc@wlu.edu

LARRY S. ROBERTS

Larry S. Roberts, Professor Emeritus of Biology at Texas Tech University and an adjunct professor at Florida International University, has extensive experience teaching invertebrate zoology, marine biology, parasitology, and developmental biology. He received his Sc.D. in parasitology at the Johns Hopkins University and is the lead author of Schmidt and Roberts's *Foundations of Parasitology,* sixth edition. Dr. Roberts is also co-author of *Integrated Principles of Zoology, Biology of Animals,* and *Animal Diversity,* and is author of *The Underwater World of Sport Diving.*

Dr. Roberts has published many research articles and reviews. He has served as President of the American Society of Parasitologists, Southwestern Association of Parasitologists, and Southeastern Society of Parasitologists, and is a member of numerous other professional societies. Dr. Roberts also serves on the Editorial Board of the journal, *Parasitology Research.*

His hobbies include scuba diving, underwater photography, and tropical horticulture.

Dr. Roberts can be contacted at:
Lroberts1@compuserve.com

SUSAN KEEN

Susan Keen is Associate Dean for Undergraduate Academic Programs, College of Biological Sciences at the University of California – Davis. She received her Ph.D. in zoology from the University of California – Davis, following a M.Sc. from the University of Michigan at Ann Arbor. She is a native of Canada and obtained her undergraduate education at the University of British Columbia in Vancouver.

Dr. Keen is an invertebrate zoologist fascinated with jellyfish life histories. She has a particular interest in life cycles where both asexual and sexual phases of organisms are present, as they are in most jellyfishes. Her other research has included work on sessile marine invertebrate communities, spider populations, and Andean potato evolution.

Dr. Keen has been teaching evolution and animal diversity within the Introductory Biology series for 15 years. She enjoys all facets of the teaching process, from lectures and discussions to the design of effective laboratory exercises. In addition to her work with introductory biology, she offers seminars for the Davis Honors Challenge program, and for undergraduate and graduate students interested in teaching methods for biology. She was given an Excellence in Education Award from the Associated Students group at Davis in 2004. She attended the National Academies Summer Institute on Undergraduate Education in Biology in 2005, and was a National Academies Education Fellow in the Life Sciences for 2005–2006.

Her interests include weight training, horseback riding, gardening, travel, and mystery novels.

Dr. Keen can be contacted at:
slkeen@ucdavis.edu

DAVID J. EISENHOUR

David J. Eisenhour is professor of biology at Morehead State University in Morehead, Kentucky. He received his Ph.D. in zoology from Southern Illinois University, Carbondale. He teaches courses in environmental science, human anatomy, general zoology, comparative anatomy, ichthyology, and vertebrate zoology. David has an active research program that focuses on systematics, conservation biology, and natural history of North American freshwater fishes. He has a particular interest in the diversity of Kentucky's fishes and is writing a book about that subject. He and his students have authored several publications. David serves as an academic advisor to prepharmacy students.

His interests include fishing, landscaping, softball, traveling, and entertaining his three children, who, along with his wife, are enthusiastic participants in fieldwork.

Dr. Eisenhour can be contacted at:
d.eisenhour@morehead-st.edu

ALLAN LARSON

Allan Larson is a professor at Washington University, St. Louis, MO. He received his Ph.D. in genetics at the University of California – Berkeley, following B.S. and M.S. degrees in zoology from the University of Maryland. His fields of specialization include evolutionary biology, molecular population genetics and systematics, and amphibian systematics. He teaches courses in introductory genetics, zoology, macroevolution, molecular evolution, and the history of evolutionary theory, and has organized and taught a special course in evolutionary biology for high-school teachers. Dr. Larson's students have participated in zoological field studies around the world, including projects in Africa, Asia, Australia, Madagascar, North America, South America, the Indo-Pacific Ocean, and the Caribbean Islands. Dr. Larson has authored numerous scientific publications, and has edited for the journals *The American Naturalist, Evolution, Journal of Experimental Zoology, Molecular Phylogenetics and Evolution,* and *Systematic Biology.* Dr. Larson serves as an academic

advisor to undergraduate students and supervises the undergraduate biology curriculum at Washington University.

Dr. Larson can be contacted at:
larson@wustl.edu

HELEN I'ANSON

Helen I'Anson, a native of England, is professor of biology at Washington and Lee University in Lexington, Virginia. She received her Ph.D. in physiology at the University of Kentucky, Lexington, and postdoctoral training at the University of Michigan, Ann Arbor. She teaches courses in animal physiology, microanatomy, neuroendocrinology, general biology, and reproductive physiology. She has an active research program that focuses on the neural regulation of reproductive development. In particular, she is interested in how energy is partitioned in the developing animal, how signals from food and food storage depots are monitored by the brain, and how such signals are transduced to regulate reproductive activity at the onset of puberty in mammals.

Her interests include gardening, hiking, fishing, aromatherapy, music, and participating in choral ensembles.

Dr. I'Anson can be contacted at:
iansonh@wlu.edu

PREFACE

Integrated Principles of Zoology continues to be the leading text for the introductory zoology course. With the sixteenth edition, the authors bring a wealth of real experience as they describe the diversity of animal life and the fascinating adaptations that enable animals to inhabit so many ecological niches.

The overall organization of this text has proven to work well to help students understand the content. Distinctive features, especially the emphasis on principles of evolution and zoological science, have been strengthened. To aid in student learning, several pedagogical features have been retained: opening chapter dialogues drawn from the chapter's theme; chapter summaries and review questions to aid in comprehension and study; concise and visually appealing illustrations; chapter notes and essays that offer interesting sidelights to the narrative; literature citations; and an extensive glossary providing pronunciations, derivations, and definitions of terms used in the text.

NEW TO THE SIXTEENTH EDITION

Phylogeny and Taxonomy

Each edition of *Integrated Principles of Zoology* brings new knowledge of phylogenetic relationships among animals and their corresponding taxonomy. Relationships among the animal phyla remain a particularly challenging phylogenetic problem, with new data often rejecting formerly favored relationships at the phylum level. We thus add several new groups to the cladogram inside the Front Cover and reorder some chapters accordingly. New taxa include Platyzoa, which unites Platyhelminthes, Gastrotricha, and Gnathifera; Polyzoa, which comprises Cycliophora, Entoprocta, and Ectoprocta; and Kryptrochozoa, uniting taxa with a "hidden" or modified trochophore larval stage. Kryptrochozoa contains Brachiopoda, Phoronida, and Nemertea. Note that the lophophorate taxa (Ectoprocta, Brachiopoda, and Phoronida) do not form a clade. To accommodate these changes, contents of Chapters 14 and 15 are reordered with respect to coverage in the fifteenth edition. Chapter 14 now presents the acoelomorphs, Platyzoa, and mesozoans, whereas Chapter 15 covers Polyzoa and Kryptrochozoa.

New phylogenetic data likewise require some major revisions of cladograms within phyla and chapters. (1) We add class Homoscleromorpha to phylum Porifera (Chapter 12). (2) Evolutionary relationships and taxonomy within phylum Annelida (Chapter 17) are completely revised, discontinuing the traditional but now clearly paraphyletic taxa Polychaeta and Oligochaeta. The terms "polychaete" and "oligochaete" continue to denote particular morphologies but not formal taxa. The basal phylogenetic split within annelids shows chaetopterid worms forming the sister taxon to the archiannelids. Many years ago, zoologists taxonomically separated errant polychaetes from sedentary polychaetes, but modern biologists rejected this dichotomy. New phylogenies resurrect this distinction, but place sedentary polychaetes in a clade with members of Clitellata. We include members of former phylum Echiura, the spoon worms, as a branch within the sedentary polychaetes and discuss the loss of metamerism implied by this position. We continue to place phylum Sipuncula outside Annelida despite some conflicting phylogenetic evidence. (3) The revised molluscan cladogram in Chapter 16 now places Aculifera (Solenogastres, Caudofoveata, and Polyplacophora) as the sister taxon to Conchifera (shellbearers). (4) Within Ecdysozoa (Chapter 18), recent work places Onychophora and Tardigrada as sister taxa, with this pair being the sister taxon to Arthropoda. We added a description of the human parasite, guinea worm, to the section on nematodes. (5) The arthropod cladogram in Chapter 19 now depicts relationships supported under the mandibulate hypothesis: all taxa sharing mandibles are united and this group is distinct phylogenetically from the chelicerate taxa. (6) The evolutionary relationships among the crustacean arthropods are revised, especially the positions of Cephalocaridea and Remipedia (Chapter 20). Some major groupings within Crustacea have not been assigned traditional Linnaean ranks (classes and orders) and are thus presented as rank-free taxa. (7) Revisions to echinoderm taxonomy (Chapter 22) include addition of newly discovered, bilaterally symmetrical fossils and a new discussion of the phylogeny of Xenoturbellida. (8) We streamline and update coverage of early tetrapod evolution, including placements of key fossil taxa on the phylogeny (Chapter 25). (9) Species diversity of amphibians (Chapter 25) is updated to include many recently discovered species. (10) We extensively revise the ordinal level taxonomy of birds (Chapter 27). (11) Results of recent fossil studies update our discussion of human evolution (Chapter 28).

We expand our coverage of molecular phylogenetics to show how approaches based on maximum-likelihood and Bayesian methods permit us to overcome simplifying assumptions in molecular evolution and thus to obtain more information from aligned DNA sequences (Chapter 10). We emphasize that our prior coverage of parsimony-based cladistic methods is a simple limiting case of the more elaborate procedures rather than a fundamental contrast of phylogenetic principles. Although these methodological advances might seem to be beyond the scope of an introductory course, most of our updates to animal phylogeny are based on these methods. Basic knowledge of statistical inference in phylogeny is thus a foundational principle of modern zoology.

Conceptual and Empirical Updates

We include revised or expanded coverage of critical concepts that we invoke repeatedly through the text. Chapter 1 includes an extensively revised discussion of science as a process, with illustrative examples. The major contrast "experimental versus comparative methods" replaces the older "experimental versus evolutionary sciences" in separating

methodological approaches for evaluating proximate versus ultimate causes. We revise our coverage of Darwinism to emphasize continuity of past and present forms as a critical part of Darwin's most basic claim of perpetual change (Chapters 1 and 6). In Chapter 10, we clarify the contrast between classification and systematization and add a citation to the original article making this contrast. We introduce for the first time in this text the "general lineage concept of species" as one that emphasizes the shared attributes of the contrasting species concepts, specifically that in each one a species has the primary definition of being a segment of a population lineage. We remove the term "traditional" from our standard reference to Simpsonian evolutionary taxonomy (Chapter 10), following a reviewer's comment that this term mistakenly implies an antiquated system.

We include throughout the text numerous updates to empirical results, methods, and interpretations of key examples. In some cases, these changes denote new widespread acceptance of claims formerly considered tentative or marginal. Our coverage of the chemistry and origin of life (Chapter 2) adds the hypothesis that early photosynthesis utilized hydrogen sulfide or hydrogen gas rather than water as source of hydrogen atoms. We add explicit coverage of hypotheses of the great oxygenation event (GOE) 2.5 billion years ago and its enormous consequences for evolution of life. In discussing the importance of water for life, we update NASA findings of ice on the moon as critical to planning a human outpost there. In our coverage of lipids, we substitute the more popular term "triglycerides" for "neutral fats."

In our evolutionary coverage, we add new information helpful for explaining what appear to be high levels of speciation in lake fishes (Chapter 6). Climatic cycles produce episodic geographic fragmentation followed by consolidation of lake-fish populations, thereby explaining how allopatric speciation can explain high fish species diversity within what is now a single lake. Also in the evolution chapter, we have rewritten the explanation of Hardy-Weinberg equilibrium to make more explicit the historical formulation and use of this mathematical principle as a null hypothesis. We extend the coverage of Hardy-Weinberg equilibrium to include more than 2 alleles, given that most molecular markers used in modern population genetics reveal multiple alleles in a population for most variable genetic loci.

Our coverage of evolutionary ecology (Chapter 38) includes a revised description of mimicry between monarch and viceroy butterflies acknowledging evidence that the viceroy is somewhat distasteful and thus might better fit the Müllerian model of mimicry rather than the Batesian model. We revise our discussion of the contrast between mass extinction and background extinction to note that the contrast is greater in the post-Paleozoic fossil record than in the Paleozoic. We add new discussion of how solar cycles can influence the timing of predator-prey cycles, illustrating interaction of density-dependent and density-independent ecological phenomena. Further coverage of population cycles of snowshoe hare appears in Chapter 28 together with updates on caribou populations and human domestication of mammals. Chapter 27 features a new, boxed essay on the effects of DDT on bird populations. Chapter 30 includes clarifications in salt and water balance in freshwater, marine, and terrestrial environments, and in invertebrate excretory structures.

Multiple updates to our physiological coverage emphasize important findings relevant to humans. We substantially modify the section on regulation of food intake (Chapter 32) to include new statistics on overweight and obese adults and children, and information on energy balance by the newly discovered hormone, irisin. Because irisin originates in skeletal muscle and is released into blood during exercise, we add skeletal muscle as an endocrine tissue in Chapter 34 and update coverage of its structure in Chapter 29. Chapter 33 includes clarifications on myelin, microglial cells, and the resting membrane potential. Chapter 35 presents new information on the innate lymphoid cell (ILC) called RORγt^+ ILC and its role in GI tract bacterial containment by secretion of interleukin 22. Revisions to Chapter 34 add a text box on G protein coupled receptors and a section on cytoplasmic receptors for lipid-soluble hormones, such as steroids. Revisions for greater clarity of explanation occur in coverage of the enteroendocrine system as a diffuse endocrine tissue, the hypothalamus and neurosecretions, and brain neuropeptides. Chapter 38 includes a revised discussion of how humans fit into the ecological food web and a new graphic showing demographic changes in Mexico. Chapter 7 includes an updated box on contraception in females, and new information on continued production of germ cells in adult mammals. Chapter 34 includes new statistics on uses of anabolic steroids by adolescents. Chapter 35 presents new statistics on the worldwide spread of AIDS. New physiological material outside the realm of human biology includes updates on invertebrate immune functions (Chapter 35), caste systems in insects (Chapter 18), and reproductive biology of hagfishes (Chapter 24).

The International Commission on Stratigraphy has greatly revised the estimated ages of many rock strata as shown on the inside back cover of the book. We have updated our figure to match their 2013 version of the International Chronostratigraphic Chart, and we have made revisions throughout the text to accommodate the new geological dates. Nonetheless, students should be aware that geological dates have changed considerably in the past two years and are likely to change again, yielding discrepancies among primary and secondary sources in the exact dates of geological strata. We have retained some presentations, such as Figure 6.12, in the form originally reported rather than trying to interpolate the effects of new stratigraphic dates on the temporal distributions of fossils. We add a footnote to Chapter 38 acknowledging that David Raup's analysis of extinction peaks would need some revision to be strictly compatible with the new dating of geological strata. Nonetheless, his major finding of episodicity of extinction peaks is robust to the revised time scale.

Pedagogy and Illustrations

Many changes serve primarily to improve pedagogy rather than adding new material. We add Latin names of species featured in illustrative examples of animal behavior, geography, and ecology (Chapters 36–38). We add specific information on the sources of examples used to illustrate cellular-level phenomena; for example, we identify the source of epithelial cells shown in Figure 1.4 as the lining of a rat oviduct. We standardize the boxed summaries of taxon characteristics in the vertebrate chapters to follow the same sequence of body systems among chapters. We convert many statements from passive to

active voice, which makes the text more engaging while decreasing its total length. We have eliminated some redundancies to shorten the text; for example, material contrasting development of protostomes and deuterostomes was removed from Chapter 10 because of redundancy with Chapter 8.

Topics revised for improved pedagogy include adding a diagram of the quaternary structure of hemoglobin (Chapter 2), which is referenced in examples using hemoglobin in other chapters. Also in Chapter 2, we expand the description of endosymbiotic origin of eukaryotic cells with an explanatory diagram. Chapter 3 features some redrawn figures and a new explanation of transport of substances across cell membranes by diffusion, osmosis, and facilitated diffusion using channels and carrier proteins. Chapter 5 presents expanded coverage of the effect of Hemoglobin S on the quaternary structure of hemoglobin (Chapter 2). We include a new figure in Chapter 5 to illustrate how polygenic inheritance produces quantitative variation in phenotype, and we have modified Figure 5.6 to make a more obvious visual distinction between tall and short plants in Mendel's experiments. Chapter 6 includes a new question instructing students to calculate allelic frequencies from allozyme data. Chapter 7 includes a new explanation of asexual reproduction, including a new text box on parthenogenesis in mammals, plus revised descriptions of oogenesis and invertebrate reproductive systems. Chapter 10 presents a new figure to illustrate the contrasting decisions that advocates of different species concepts would make in handling taxonomically challenging situations (hybridization, asexual reproduction). This exercise will help students to appreciate the complexity and ambiguities commonly encountered in taxonomic recognition of species. Chapter 10 features an important new reference to David Baum and Stacey Smith's recent book *Tree Thinking,* which is particularly helpful in teaching students how to interpret and to use phylogenetic trees.

Organismal coverage features new graphics and highlights on particularly interesting taxa. To Chapter 11 we add a brief discussion of giant multinucleate foraminiferans called xenophyophores. These organisms reach 20 cm in diameter and collect small particulates into a test. Their fecal pellets often contain heavy metals such as lead and they concentrate barium in the cytoplasm. We also have replaced the life-cycle diagram of a colonial species of *Volvox* with an illustration of the lifecycle of the multicellular *Volvox carteri*. This photosynthetic eukaryote exemplifies one of the 25 known cases where multicellularity has evolved independently. In Chapter 12 we have added the astonishingly complex harp sponge, *Chondrocladia lyra*, to our discussion of Porifera and included a photograph. This deep-sea sponge is surprising in its morphology, mode of feeding, and reproductive biology. We also have added a new drawing of the morphology of a hexactinellid sponge. Many arthropod photos have been updated, including a new photo of a camel (wind) spider (Chapter 19). Chapter 20 features a new photograph of a giant (40 cm) deep-sea isopod. Many photographs of the echinoderms in Chapter 22 have been replaced with better ones, and a new note describes ranching of sea cucumbers. We expand coverage of venomous snakes (Chapter 26) and avian flight (Chapter 27) with new figures. Improved photographs illustrate sexual dimorphism in wood ducks (Chapter 6), penguins as an adaptive zone (Chapter 10), and otter as an important predator on sea urchins in oceanic kelp forests (Chapter 37). Improved graphics include illustrations of frog reproductive modes (Chapter 25) and mammalian dentition (Chapter 32).

TEACHING AND LEARNING AIDS

To help students in **vocabulary development,** key words are boldfaced and derivations of technical and zoological terms are provided, along with generic names of animals where they first appear in the text. In this way students gradually become familiar with the more common roots that form many technical terms. An extensive **glossary** provides pronunciation, derivation, and definition of each term. Many new terms were added to the glossary or rewritten for this edition.

A distinctive feature of this text is a **prologue** for each chapter that highlights a theme or fact relating to the chapter. Some prologues present biological, particularly evolutionary, principles; those in Part Three on animal diversity illuminate distinguishing characteristics of the group presented in the chapter.

Chapter notes, which appear throughout the book, augment the text material and offer interesting sidelights without interrupting the narrative. We prepared many new notes for this edition and revised several existing notes.

To assist students in chapter review, each chapter ends with a **concise summary,** a list of **review questions,** and **annotated selected references.** The review questions enable a student to self-test retention and understanding of the more important chapter material.

Again, William C. Ober and Claire W. Ober have strengthened the art program for this text with many new full-color paintings that replace older art, or that illustrate new material. Bill's artistic skills, knowledge of biology, and experience gained from an earlier career as a practicing physician have enriched this text through 10 of its editions. Claire practiced pediatric and obstetric nursing before turning to scientific illustration as a full-time career. Texts illustrated by Bill and Claire have received national recognition and won awards from the Association of Medical Illustrators, American Institute of Graphic Arts, Chicago Book Clinic, Printing Industries of America, and Bookbuilders West. They are also recipients of the Art Directors Award.

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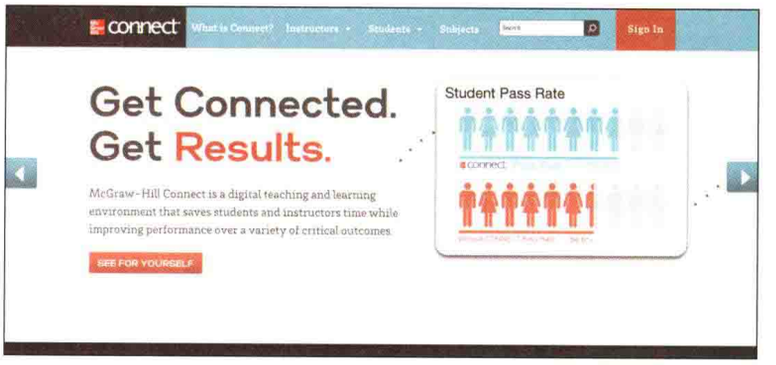

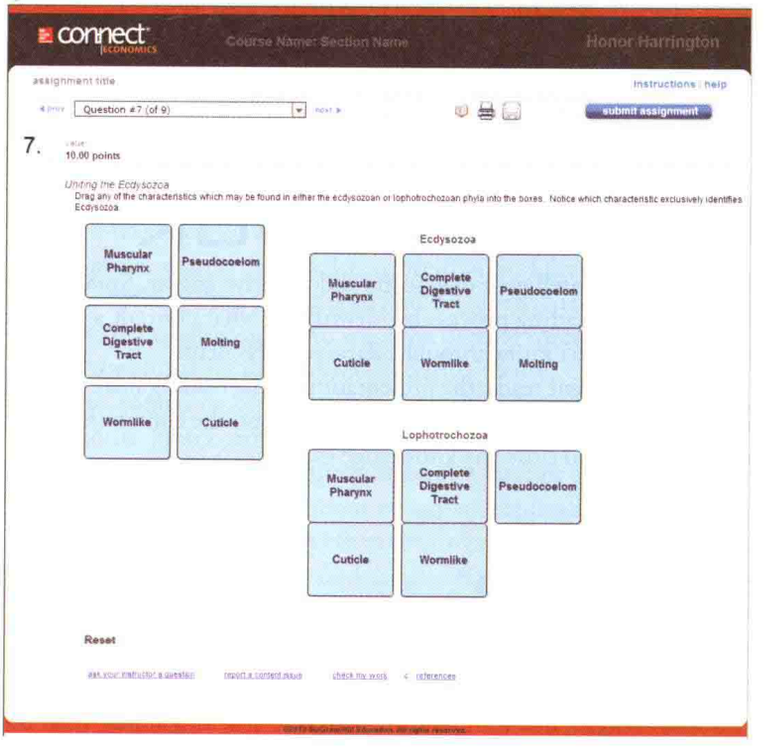

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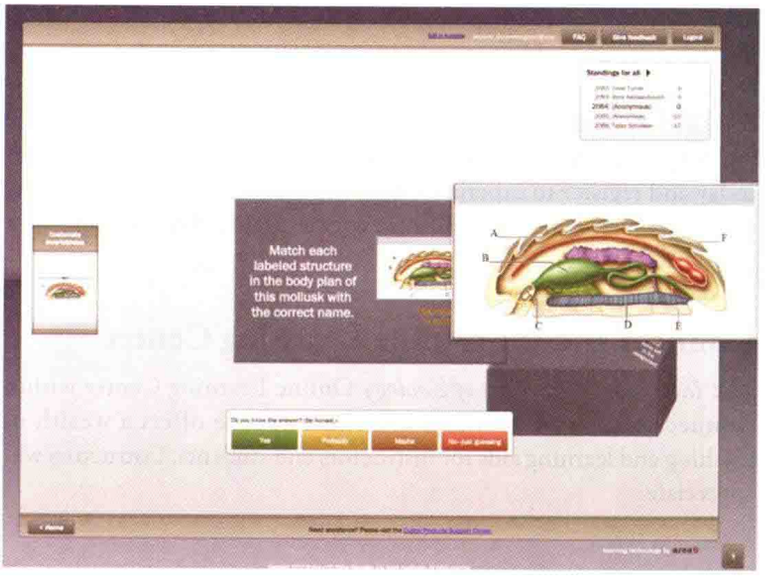

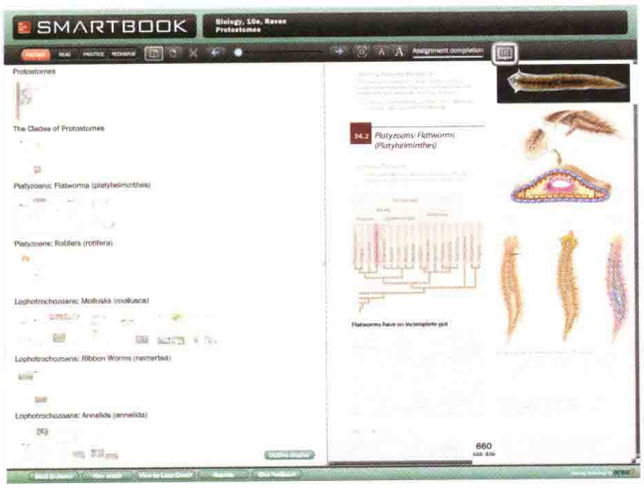

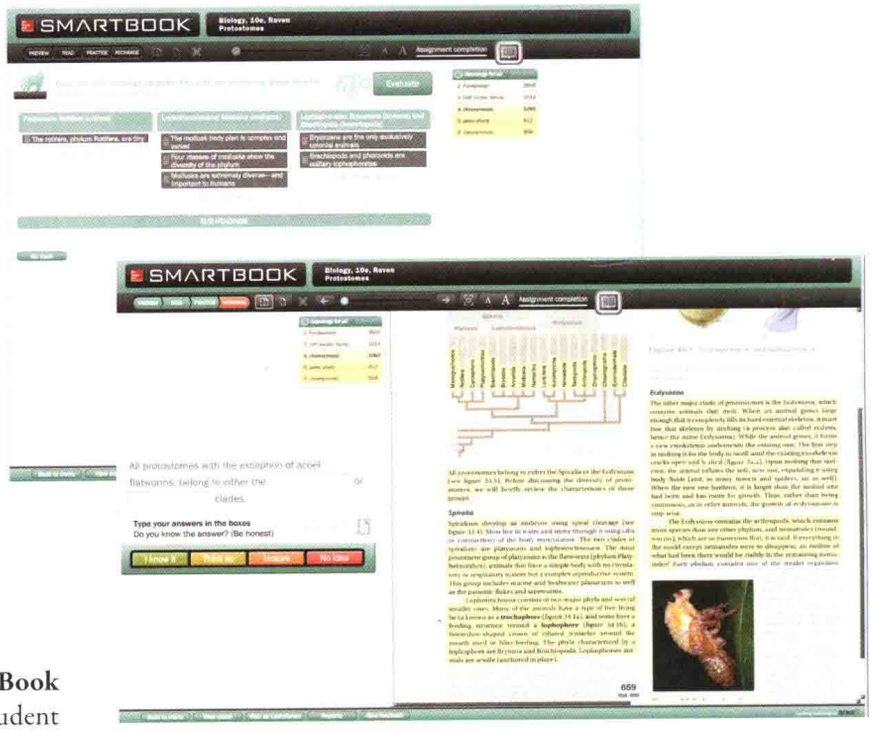

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Connect and the Online Learning Center

The *Integrated Principles of Zoology* Online Learning Center within Connect or at www.mhhe.com/hickmanipz16e offers a wealth of teaching and learning aids for instructors and students. Instructors will appreciate:

- A password-protected Instructor's Manual and Test Bank

  The **Instructor's Manual** provides chapter outlines, lecture enrichment suggestions, lesson plans, a list of changes from the previous edition, and source materials.

  The **Test Bank** utilizes testing software to create customized exams is available with this text. The user-friendly software allows instructors to search for questions by topic or format, edit existing questions or add new ones, and scramble questions to create multiple versions of the same test. Word files of the test bank questions are provided for those instructors who prefer to work outside the test-generator software.
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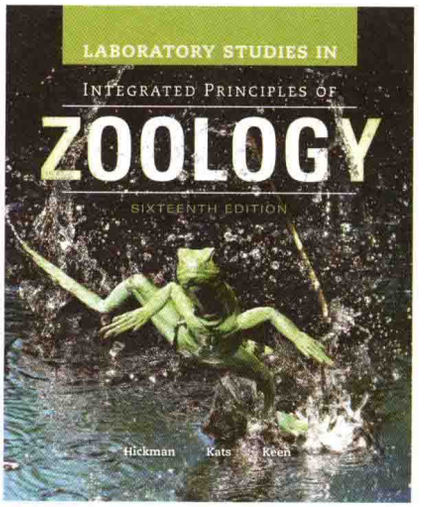
Students will appreciate:

- Online activities such as chapter quizzing and key term flash cards!

For the Zoology Lab

Laboratory Studies in Integrated Principles of Zoology **by Cleveland Hickman, Jr., Susan Keen, and Lee B. Kats**

Now in its sixteenth edition, this lab manual was written to accompany *Integrated Principles of Zoology,* and can be easily adapted to fit a variety of course plans.



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Although we make every effort to bring to you an error-free text, errors of many kinds inevitably find their way into a textbook of this scope and complexity. We will be grateful to readers who have comments or suggestions concerning content to send their remarks to Patrick Reidy, Executive Marketing Manager, at patrick.reidy@mheducation.com

Cleveland P. Hickman, Jr.
Larry S. Roberts
Susan Keen
David J. Eisenhour
Allan Larson
Helen I'Anson

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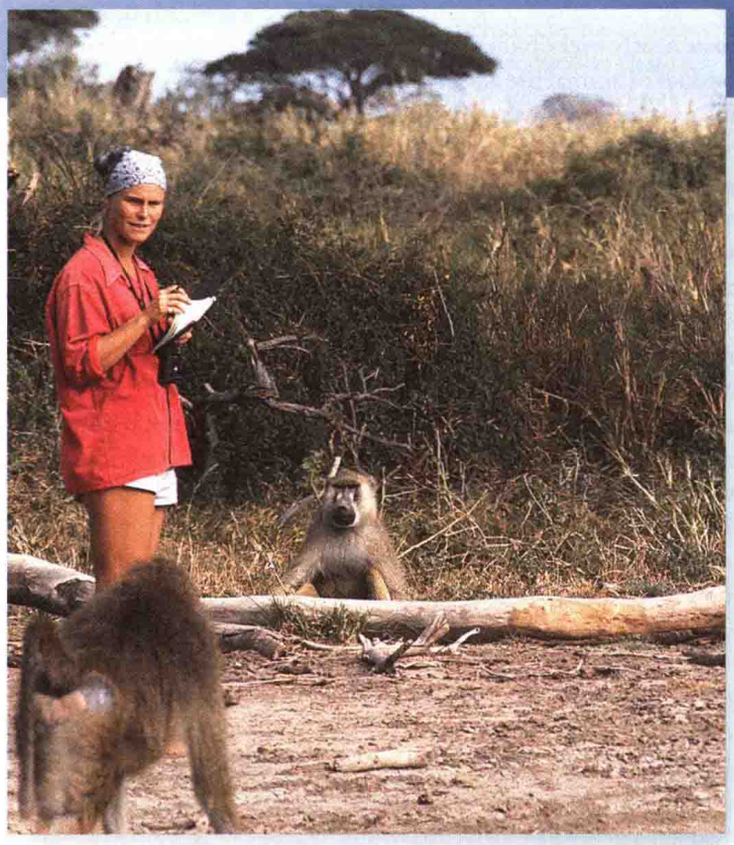
PART ONE

CHAPTER 1

Life: Biological Principles and the Science of Zoology



Zoologist studying the behavior of yellow baboons (Papio cynocephalus) *in the Amboseli Reserve, Kenya.*

The Uses of Principles

We explore the animal world by actively applying important guiding principles to our investigations. Just as the exploration of outer space is both guided and limited by available technologies, exploration of the animal world depends critically on our questions, methods, and principles. Zoology makes sense to us only when we understand the principles used to construct this knowledge.

The principles of modern zoology trace their long history to many sources. Some principles come from laws of physics and chemistry, which all living systems obey. Others come from the scientific method, which tells us that our hypothetical explanations of the animal world must guide us to gather data that potentially can refute these explanations. Many important principles come from previous studies of the living world, of which animals are one part.

Principles of heredity, variation, and organic evolution guide the study of life from the simplest unicellular forms to the most complex animals, fungi, and plants. Because life shares a common evolutionary origin, principles learned from the study of one group often provide insights into other groups as well. By tracing the origins of our operating principles, we see that zoologists are not an island unto themselves but part of a larger scientific community.

We begin our study of zoology by searching broadly for our most basic principles and their diverse sources. These principles simultaneously guide our studies of animals and integrate those studies into the broader context of human knowledge.